Male reproductive strategy basics:

- Males are not forced to invest a lot in their offspring, the way females are
  - males can have almost unlimited numbers of offspring
  - so male reproductive success can vary over a much wider range than females' reproductive success
  - in a typical species, females might range from zero to five offspring
  - in the same species, males might range from zero to fifty offspring
  - all females can mate as often as they need to - they virtually all reach their limit of pregnancies per lifetime
  - food, not access to mates, is the main limiting factor for females
  - but the more a male mates, the more offspring he has
  - in some cases, it may be to the male’s advantage to care for offspring, but this is rare
  - in mammals such as primates, usually selection will tend to favor traits in males that lead them to mate frequently

Sexual selection: selection that favors traits that increase male success in mating

- Sexual selection is just a kind of natural selection
  - but it is unusual in that it often favors traits that
  - are mostly or only expressed in males
  - and that seem to be useless or even harmful to the males’ survival
  - the huge tails of male peacocks, for instance
    - that make it hard for the peacocks to escape predators
    - but make them more attractive to female peacocks
  - sexual selection favors traits like these if
    - if they improve the males’ reproductive success by increasing matings
    - more than they harm reproductive success by increasing predation or other costs

- two kinds of sexual selection:
  - intrasexual selection: selection that occurs due to differences in success at mating that result from interactions between members of the same sex
    - the most common form is male-male competition
      - such as males fighting each other for access to females
      - the outcome of the interaction of the males determines which male mates; the female is not involved in the decision
    - example: intrasexual selection might lead to large canines becoming common among males, because the males with the largest canines can drive other males away, so they get more access to females, so they leave more offspring
  - intersexual selection: selection that occurs due to differences in success at mating that result from interactions between members of opposite sexes
    - the most common form is female choice
      - such as females picking the most desirable male to mate with, based on some visible trait
example: intersexual selection among peacocks might lead to large tails becoming common among males, because the female peacocks prefer to mate with males with large tails, so the large-tailed males mate more often, so they leave more offspring.

other kinds of natural selection caused by predators, changing food supplies, etc. act more or less equally on males and females

but sexual selection acts primarily on the one sex that is competing for the other

that is, it mostly affects males

recall that female mammals can have only a limited number of offspring, but males have almost no limit

females can generally only conceive when they aren't pregnant or lactating, and even then only during a limited portion of their cycle

males can mate any time

so there are generally plenty of males around to mate with when a female needs to

but the males have to compete for access to those limited chances to father offspring

so selection will favor any feature of the males that increases their success at mating

we tend to think of survival to adulthood as being the biggest factor in natural selection, hence the phrase "survival of the fittest"

a phrase that does not even appear in Darwin's *Origin of Species*

but in fact, sexual selection can exert a much stronger evolutionary effect than selection based on different rates of survival

males who do not mate frequently may produce absolutely no offspring

this means absolutely none of their genes go into the next generation -- very severe selection against their traits

from an evolutionary point of view, leaving no offspring is equivalent to dying in infancy

yet, it is common for males to have no offspring

meanwhile, males who mate often may produce many, many offspring

very rapidly increasing the representation of their traits in the next generation

being successful at mating and having a large number of offspring has a far greater effect that just surviving and having an average number of offspring

example: imagine a species in which 80% of the males produce no offspring, and the remaining 20% father the entire next generation

these are realistic figures for many animals, from lions to baboons

the effect of this difference in just one generation would be equivalent to a drought that killed off 8 out of 10 individuals - a very drastic selection event

that is, an ordinary, common amount of selection on sexual success has as much effect on the next generation as the most drastic, rare extremes of selection that affect survival

the same is true even if most males do leave one or two offspring, as long as a few have large numbers of offspring

say ten males have one offspring each, and one male has a dozen

that one male contributes more genes to the next generation that all the rest of the males combined!

the traits that led him to have many children are much more common after a single generation!
Point: the process that has the strongest, most consistent effect on evolution is not "survival of the fittest", but "mating of the sexiest"

because sexual selection is so strong, it can favor traits that have significant costs for survival

classic example of sexual selection: peacock tails (on males)
– the showier the tail, the more successful the male is at mating
– the tails have gotten so big that they make it hard for the males to hide or get away from predators
– but the benefit in terms of success in mating outweighs the cost to survival

intrasexual selection (male-male competition) in primates
– males try to keep other males away from females
– this ensures that they are the likely fathers of any offspring
– this involves hostile encounters or fights
– so sexual selection favors large body size, large canines, possibly other traits in males that help one male defeat another for access to females
– but females would not benefit as much from larger body size, canines, etc.
– they would just have to eat even more to maintain a large body
– when food is already their limiting factor in reproductive success

since selection favors larger males but smaller females, eventually sexual dimorphism arises
– differences between males and females
– sure enough, those species with the greatest male-male competition have the greatest sexual dimorphism
– male-male competition is assumed to be greatest in species whose social groups have the greatest imbalance of females to males
– because if there are relatively few males in the group, mating with the many females, then there must be lots of males excluded from the group who are not mating at all
– these bachelor males must be constantly driven away by the few males in the group
– the evidence:
– in monogamous species there is very little male-male competition, since each male is paired with one female
– and indeed, monogamous species have almost no sexual dimorphism
– gibbons and siamangs are a classic examples; try telling the males from the females at the zoo!
– in multi-male, multi-female groups, there is considerable male-male competition
– sexual dimorphism is marked
– baboons are a classic example
– note the much bigger bodies of the males, their big canine teeth, and intimidating "mane"
– in single-male, multi-female groups, male-male competition is the most intense
– the single male has to defend the whole group from circling bachelor males all the time
− but as long as he can do so, he is rewarded with tremendous reproductive success, compared to the others who don't mate at all
− species that form single-male, multi-female groups have the most extreme sexual dimorphism
− gorillas are a classic example
  − gorillas often form single-male groups, but sometimes also include one or even two subordinate males
  − gorilla males are much bigger than females, more robust, aggressive, etc.
− So consider humans…
− compared to most apes, we have minimal sexual dimorphism
− human males are only a little larger than human females, and are only mildly better suited to fighting each other
  − no big canines
− nothing like the difference between male and female gorillas, baboons, etc.
− so humans presumably evolved in social groups with relatively little male-male competition
− probably mostly monogamous pairs
  − so monogamy is not a recent, casual invention for humans
  − it is the mating system that must have prevailed for at least the later part of our physical evolution
  − humans did not evolve in a social setting like that of baboons or gorillas
− of course, even though the bulk of the matings were probably within monogamous pairs, that would still be just the general rule
  − it does not mean that the membership of these pairs did not shift over time, or that there was no cheating
− mating strategies also affect sperm production
− in most primates, females only mate during the part of their cycle when they can conceive: **estrus** (the period when they are “in heat”)
− if there are multiple males around, a female could mate with several males during a single estrus period
− which one is most likely to father her infant?
  − even a small number of sperm is enough to get the female pregnant; it only takes one
  − whichever male deposits the most sperm will have the most chance of being the father of the offspring, just by increasing his odds in the random selection that will occur
− so in multi-male, multi-female groups, where multiple males mate with each receptive female, whichever male puts out the most sperm will tend to father the most offspring
  − so in multi-male, multi-female groups, sexual selection favors greater sperm production
    -- larger testes
  − this is not an issue in single-male, multi-female groups
  − since the one male is keeping all the other males away
  − so males of species with single-male, multi-female mating patterns tend to have small testes for their body size
  − even though they tend to be the ones with the biggest canines and the greatest dimorphism in body size
− it is also a minor issue for primates who live in monogamous pairs
− since only one male is mating with the female
− but for some reason, males of "monogamous" species tend to have larger testes for their body size than do males of single-male, multi-female groups
− what might this suggest about the effectiveness of these two strategies for monopolizing access to the females?
− this is something you might look for at the zoo, especially if you bring binoculars.

Compare the size of testes of:
− male baboons or male chimps, who live in multi-male, multi-female groups
− to male gorillas (at the SF zoo), who live in single-male groups (or groups in which sub-dominant males do not mate with the females)
− try explaining this to the people standing near you and see what happens!

− intersexual selection (mostly female choice) in primates
− since receptive females are scarce and males are plentiful, females can be picky about which males they mate with
− they don't have to mate with any particular male, since there are plenty of others to choose from
− in contrast to males, who benefit from mating with any female they can find
− so selection will favor any traits that make a male more likely to be acceptable to a female
− but why would selection favor picky females?
− why would a female leave more surviving offspring by not mating with the first male that came along?
− three general reasons:
  − 1. some males might have genetic traits that, when inherited by the offspring, would help it be more successful (mature faster, be healthier, etc.)
    − any tendency of females to select males with these traits will be favored by sexual selection
    − so females will tend to develop preferences for any traits that indicate these characteristics
    − for example, large tail feathers might indicate healthier males
    − so females that tend to mate with males with large tail feathers would produce healthier offspring, and their preference would be selected for
  − 2. some males might have traits that benefit the female's survival and that of her infant
    − some males might be more prone to vigorously defend her and her offspring from predators, or to defend a larger territory so that she has more food to eat
    − any tendency of females to select males with these traits will be favored by sexual selection
    − because females who tend to mate with males with traits related to these features, like aggressiveness, will leave more surviving offspring than those that do not
  − 3. Any tendency by females to prefer males with particular traits – for any arbitrary, even non-adaptive reason – can take off very quickly and become a strong preference
− Imagine that some females prefer males who tend to defend them
− so more females mate with defending males
so the defending males leave more offspring
this has two effects at once
the females who preferred the traits leave more offspring because the trait improved
the survival of themselves and their offspring, so:
the tendency to prefer males who have the trait becomes more common among
females
the males who have the trait leave more offspring because more females mate with
them, so
the trait itself becomes more common among the males
so both the preference among females, and the preferred trait among males, become
more common at the same time
This is easy enough to see if the trait has a real value. But any incipient pickiness about
any trait can get exaggerated beyond its real value to reproductive success
in a process sometimes called "runaway" sexual selection
say a few females tend to mate more often with brighter-colored males
for some basically unimportant reason
for example, maybe the color causes them to look at those males slightly more often
their female offspring often get the alleles for the preference, since the mother had the
preference
but the female offspring also get the alleles for being more colorful
although as females, they don't express them
their male offspring often get the alleles for being colorful, since the father has that
trait
but the male offspring also get the allele for the female preference
although as males, they don't express it
when females are picky about mates, the offspring tend to have both the trait they
selected and their preference for that trait
in the next generation, some females get the preference for brighter-colored males again
this time, their female offspring get alleles for the preference not only from the
mother, but also from the father
the male offspring get the alleles for the trait from both the father and the mother
so each generation that the females prefer the trait
the females in the next generation prefer it even more
and the males in the next generation have it even more
the stronger the preference for the trait, the stronger the selection for more and more
extreme expressions of it
this process simultaneously selects for the trait in the males and the preference for it in
the females
the process can spiral on to extremes that have serious costs for survival
leading to weirdly exaggerated male characteristics
like big peacock tails
or huge antlers on elk
or the colorful faces of mandrills
how can we tell if female choice was important?
– if a visible trait is found only among males and it does not seem to be related to male-male competition
– example: fleshy noses of proboscis monkeys
– female-choice intersexual selection has been shown to be important in many non-primate species
  – there are some primate species in which it may have played a role, too
    – mandrills, proboscis monkeys, maybe some features of some baboons like the large “mane”
    – but it seems to less prevalent in primates than intrasexual selection with male-male competition
– other kinds of behavior are affected by sexual selection, too
  – selection acts differently on males, depending on their mating strategies
  – monogamous males
    – little competition for females, so little sexual selection
    – one way for males to increase their reproductive success is to invest in their offspring, by carrying them, giving them food, etc.
      – this presumably increases the odds of the offspring surviving to adulthood
      – this could have a big impact on the evolution of a capacity for learned behavior
      – some monogamous species do this, others don’t
    – another way to increase reproductive success: cheat
      – it increasingly looks like "monogamous" males do in fact mate with other females occasionally
      – although most of the offspring are still from the main mate
    – the flip side of male cheating is that males benefit from preventing their mate from cheating
      – in fact, some of the male investment in offspring may pay off more in keeping the female nearby and under the male’s control than in increased survival of the offspring
      – monogamous male gibbons groom their mates much more than they get groomed back
        – suggesting that this one-sided attention may also be a way of keeping the female from going off and mating with another male
  – one-male, multi-female groups:
    – the lone male constantly has to fend off bachelor males trying to drive him away
      – in some species, the bachelor males form groups that drive off the male in a one-male, multi-female group
        – then the bachelor males fight to replace him
        – in this case, selection could be strong for abilities related to cooperation, good "political" judgement about allies and enemies
        – these conflicts are very serious, often resulting in serious injuries
        – but the payoff is monopoly access to a number of females for a while
        – any given male may not remain in a multi-female group very long
      – some bachelor males employ a different strategy to produce offspring
        – sometimes referred to as the "sneaky f***er" strategy
        – they will hang around a social group, often alone rather than with other males
when the lone male in the group is distracted or one of the receptive females is a little away from the group, the bachelor male will take the opportunity to try to mate

if some males succeed at this, selection will favor be favoring a very different set of characteristics than those present in the offspring of the lone male in the group

the lone male is typically a strong, aggressive one able to drive off other males

the successful "sneaky f***er" bachelor male might be stealthy, observant, smaller, faster, etc.

this could maintain more variation in the species, which makes them able to evolve more quickly in response to new environmental pressures, diseases, etc.

multi-male, multi-female groups:

two kinds of male-male competition:

1. between member males and nonmember males for access to females
   - bachelor males hang around the edges of the group, trying to mate with the females
   - or outsider males charge right into the group and confront the resident males

2. between member males within the group for access to females
   - males try to drive other males away from females
   - interrupt mating

or males may establish dominance relationships through spontaneous confrontations not directly related to access to females

- these establish which males are dominant over which others
- confrontations vary from stylized threats, with one male backing down, to real fights
- the vanquished male typically acknowledges this by a stereotypical gesture of submission
  
- sometimes this is a facial expression, or a posture like resting on the "elbows" of the forelimbs in order to lower the head, or a particular kind of sound
- selection favors these signaling behaviors because those that use them are less likely to get beat up in fights - they survive to try again later

- in many cases, the dominance relationships are stable, and a dominance hierarchy is formed
  
- similar to the dominance hierarchies among females
    - which give the dominant females better access to resources
- male dominance probably gives males better access to females
  - but this has only been proven for a few species so far
  - and some studies of captive primates seem to show that dominance does not improve reproductive success
  - sometimes the dominant male spends so much effort fighting to maintain his position that the second-ranked male actually has higher reproductive success
    - why would natural selection lead to this?

males may form social alliances to get access to females

- a high-dominance male will form a "consortship" with a female in estrus
  - he stays with her, grooms her, mates with her, and keeps other males away
  - this behavior assures that the offspring is his

- two less-dominant males may team up as a "coalition" to challenge the consorting male
they can often succeed in driving off the more dominant male
and one of the allies becomes the female's consort

Infanticide
when a male is driven away from a single-male, multi-female group, the new male will sometimes kill some or all of the infants
this has now been observed in numerous species
Hanuman langurs
Red howler monkeys
gorillas
chimps
the females who have lost their infants stop lactating and become receptive quickly
so the male can quickly father numerous offspring
males that do this leave more of their own alleles in the next generation; so selection favors it
this makes the most obvious sense in single-male groups, but it is now clear that infanticide happens in multi-male groups, too
for the same reason:
if a male is new to the group, or has recently moved up in the dominance hierarchy, few or none of the current infants are his
killing an infant causes the female to stop lactating and start ovulating again
so the new male has a chance of fathering her next infant
evidence that supports this explanation
new males kill infants only when they first arrive; they quickly stop killing infants before any of their own can be born
Boyd and Silk express this same concept in a different way, noting that in numerous studies, males are shown to kill primarily infants that must have been conceived before they joined the group
as determined both by the date of arrival of the male versus the age of the infant
and by DNA tests of the males and the dead infants
note that this does not necessarily mean the males can recognize their own infants
it may just mean that they tend to kill infants when they first arrive, then taper off
new males mostly kill the young infants that are nursing, whose deaths will make their mothers become receptive quicker
they don't bother with older juveniles who are no longer impeding their mother's fertility
observations in several species show that the infanticidal males frequently do mate with the females whose infants they have killed
infanticide plays a major role in evolution of some primates
in several species, up to a third of all infant deaths are infanticide
this has a big effect on r.s. of the mothers, and of the fathers
selection presumably would favor female behaviors to minimize infanticide
mothers in some species form “friendships” with certain males after they give birth, staying near them and grooming them frequently
these males may defend the infant from other males
– note that this is the exact opposite from the grooming behavior in monogamous primates, where it is males who do most of the grooming
– presumably these “friendships” pay off for the males’ r.s. in some way
  – they benefit a little from the grooming, but not much
  – but mostly, such friendships may tend to be between individuals who have recently mated, meaning that the infant may be more likely to the the male’s own offspring
  – in that case, the male is increasing his r.s. by helping his own infant to survive
  – this investment by the male is called **parenting effort**
  – friendships may also increase the likelihood of mating in the future
    – this investing by the male is called **mating effort**
– females mate with multiple males, even during pregnancy, when the male can’t actually become the father
  – this reduced the males’ clues about whether or not they are the father
  – it increases the odds that any given male in the group is the father
  – so it increases the costs to a male of killing infants, since they might be his own
– consider humans
  – human females are unusual in that they have “concealed ovulation”
  – males cannot generally tell when females can actually conceive an offspring
  – and females are receptive to sex throughout their cycle
    – they don’t have obvious periods of estrus (being “in heat”)
  – this makes it hard for males to know who the father of the female’s offspring is
  – it makes it even more important for the male to keep an eye on the female, to keep other males away
  – this would have several benefits for the female’s r.s.
    – reduces likelihood of the male committing infanticide
      – by increasing the likelihood that the infant is the males’ own offspring, since he can’t tell for sure
      – increases the male’s likelihood of staying nearby, helping to defend patches of food, defend the infant from other males, etc.
      – by making it beneficial to the male to mate more or less constantly, increasing their odds of being the father of the next offspring
        – since he can’t tell when the female can actually conceive
        – by making it more important to the male’s r.s. to keep other males away
        – these benefits to the male reduce the cost of losing opportunities to mate with other females
– female choice may also play a role in multi-male, multi-female groups
  – in some species, females prefer dominant males
    – apparently because dominant males have better access to food, and males allow their own offspring to feed near them
    – so the offspring of a female that mates with a dominant male have better access to food, grow faster, etc.
  – in others, such as some macaques, some females prefer unknown, lower-ranking males to dominant ones
since the dominance hierarchies are long-lasting, this may be beneficial to a female's reproductive success because it adds different genes to her offspring -- increases variability

Point: Sexual selection can explain how a lot of complex social behaviors evolved

- many aspects of sexual selection may have favored individuals who were more able to make complex judgments about dominance, mating opportunities, etc.
- generally more complex than behaviors related to getting food or avoiding predators
- this in turn would favor physical and behavioral traits that promote abilities and opportunities to learn, to come to correct conclusions, and to remember relevant information about many different individuals in the group
- that is, sexual selection probably played a major role in the evolution of our big brains and complex behavior

Points for specifically human evolution: Our ancestors probably evolved in monogamous social groups

- based on our minimal sexual dimorphism
- and testes size relative to body size in the intermediate range - not as big as in multi-male, multi-female groups, but not as small as in single-male, multi-female groups
- so male-male competition was probably not a big factor in the evolution that led to humans
- nor is there evidence of drastic female-choice sexual selection
- humans have no weird, functionless features like mandrills or proboscis monkeys do
- at least in this male's opinion!
- but behaviors of monogamous primates, especially mate guarding and parental investment, probably did play a major role in our evolution
- mate guarding among monogamous primates would be a kind of intrasexual selection
- but not direct male-male competition
- parental investment among monogamous primates would be a kind of intersexual selection
- in that increases the likelihood of fathering the female’s next offspring
- but not quite what we usually mean by female choice

Many of these sexual selection arguments apply to modern humans, too

- but remember, we are talking about biologically evolved tendencies, not specific behaviors or individuals, and it is all conditioned by a lot of learned behavior, including cultural norms
- but still, can you see why the following observations make good sense in light of sexual selection?
- there are a lot more male customers for female prostitutes than vice versa
- most bars are said to attract a lot of men, but not as many women (I wouldn't know, myself)
- stepchildren and adopted children are far more likely to be subject to domestic violence than are children living with their biological parents
- if you immediately think of social and emotional reasons for this, stop and think: why do we have those emotional responses that make this seem like an unsurprising fact?